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A New View on Grasping

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Reaching out for an object is often described as consisting of two components that are based on different visual information. Information about the object's position and orientation guides the hand to the object, while information about the object's shape and size determines how the fingers move relative to the thumb to grasp it. We propose an alternative description, which consists of determining suitable positions on the object—on the basis of its shape, surface roughness, and so on—and then moving one's thumb and fingers more or less independently to these positions. We modeled this description using a minimum-jerk approach, whereby the finger and thumb approach their respective target positions approximately orthogonally to the surface. Our model predicts how experimental variables such as object size, movement speed, fragility, and required accuracy will influence the timing and size of the maximum aperture of the hand. An extensive review of experimental studies on grasping showed that the predicted influences correspond to human behavior.

***Key Words*:** finger movement, grip, arm movement, kinematics, minimum-jerk model, motor control, prehension, visuomotor coordination

The study of motor control tends to focus on simple movements such as elbow flexion and finger tapping. One reason for doing so is that it is clear which variable is of interest: the elbow angle or the position of the fingertip. Grasping is a complex movement involving rotations of several joints and more than one end-effector. When interpreting grasping movements, one has to select the variables to study and motivate one's choice. Jeannerod (1981) proposed one such selection. He hypothesized that there are two independent visuomotor channels: one controlling the *transport* of the hand, the other the size of the *grip*. This description is not only convenient for describing the data but also the two variables are regarded as being the ones that are controlled during grasping (Arbib, 1981). This "classical approach" has allowed tremendous development in the research in grasping.

The main reason for finding this description so attractive is that the two channels correspond nicely to two distinct anatomical structures and to two distinct types of perceptual information. However, as we will discuss in the first section, this attraction disappears when one tries to formalize the description. Our alternative lacks the nice correspondence between information and anatomy, but it has another appeal: it does not need a special category of movements to describe

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grasping. In our alternative, grasping is nothing more than pointing with the thumb and finger toward selected positions on the surface of the object. In the second section, we will discuss and model our alternative description. In the third section, we will compare the parameters of the simulated grasping movements with a collection of published experimental results. In the fourth and final section, we will discuss the implications of this model for an understanding of the control of grasping.

1 — Shortcomings of the Classical Approach

According to the classical approach, the grasping movement can be divided into two distinct components. Viewed from an anatomical perspective, the wrist moves toward the object (*transport component*) independent of the preshaping of the fingers (*grip component*). Viewed from an informational perspective, the transport component is based on extrinsic properties of the object, whereas the grip component is based on intrinsic properties. Although this division seems very attractive, it has some severe shortcomings.

1.1 Intrinsic and Extrinsic Properties

The main theoretical argument in favor of the classical description is that information can be processed in two independent visuomotor channels (Jeannerod, 1981). In one channel, information about intrinsic object properties is processed. Such properties are independent of the relationship between the object and its environment. Examples are size, mass, shape, and color. The size of the grip is believed to be regulated using this information, primarily on the basis of the perceived size of the object. In the other channel, information about extrinsic object properties is processed. These properties describe the relationship between the object and its environment; examples are position and orientation. This information is believed to determine the transport of the wrist and orientation of the hand.

Although orientation was originally classified as extrinsic (Jeannerod, 1981), it is sometimes considered to be intrinsic (Jeannerod et al., 1995), or part of a separate third channel (Stelmach et al., 1994). This problem with classifying orientation reveals a more severe problem with the proposed segmentation. Most objects are not completely symmetrical. If the orientation of the object changes, the subject may have to modify the size of the final grip aperture (compare Figures 1A and 1B). Alternatively, the subject may change the orientation of the grip (compare Figures 1A and 1C). Objects with the same extrinsic and intrinsic properties can thus be grasped in various ways (compare Figures 1B and 1C). These different ways of grasping give rise to different sizes of the final grip, different orientations of the hand, and different positions of the wrist. Therefore, when an object is grasped using different positions for the digits on its surface, both the grip size and position of the wrist will change, although neither the intrinsic properties (size and shape) nor the extrinsic properties (position and orientation) have changed. When planning a grasping movement, the classical two components strongly depend on each other.

Grip size therefore depends on both intrinsic and extrinsic properties of the object, as well as on the transport component of the movement. This dependence is much stronger than the dependency in timing already acknowledged by Jeannerod

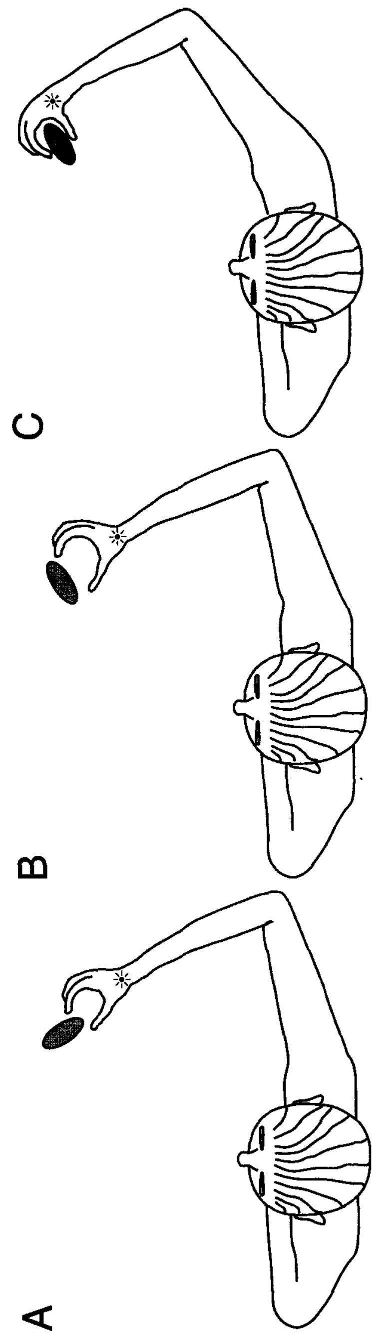

Figure 1 — The subjects in A, B, and C grasp the same object (same intrinsic properties size and shape) at the same location. The only difference between A and B is the (extrinsic) orientation of the objects. The grip size that is suitable for grasping the object in A is much smaller than that in B. The only difference between B and C is the position of the wrist. The grip size that is suitable for grasping the object in C is much smaller than that in B.

(1981). It therefore disrupts the independence between the two proposed visuomotor channels, eliminating one of the main theoretical arguments for this particular segmentation.

1.2 Anatomy

A second theoretical argument used in favor of the classical description is that the two components of behavior correspond nicely to distinct anatomical substrates at the levels of joints, muscles, and corticospinal connections. The grip consists of moving the fingers by activation of distal muscles, the motoneurones of which receive input from corticospinal projections. The hand is transported by moving the shoulder and elbow by activation of proximal muscles, the motoneurones of which do not receive direct input from corticospinal neurones. The control of these two types of muscles is indeed quite different during human grasping. For instance, Lemon et al. (1995), using transcranial magnetic brain stimulation, showed that the main cortical involvement with the distal muscles occurs later than with the proximal muscles.

A first objection to the anatomical argument is that the distinction between proximal and distal at the level of muscles is not the same as at the level of joints. Movements of the distal joints in the fingers are made not only by activating the intrinsic muscles of the hand (which are categorized as distal), but also by activating the polyarticular muscles in the lower arm (which are categorized as proximal). One could even argue that (proximal) extrinsic hand muscles take care of the orienting and preshaping of the fingers, and that (distal) intrinsic hand muscles come into play only when the object is to be touched (Lemon et al., 1995).

A second objection concerns the definition of the transport component in relation to the anatomy. A straightforward implementation is to define the transport component as the average of the positions of thumb and finger, and the grip as the difference between these positions. Another possibility is to define the tip of the thumb as being transported, as advocated by Wing and colleagues (Haggard & Wing, 1997; Wing & Fraser, 1983; Wing et al., 1986). In both cases, the transport component depends on the movement of the digits, so that the division between the components does not correspond with anatomical entities.

Most authors avoid this problem by defining the transport component as the movement of the wrist. In this way it only depends on movements of the arm, not of the fingers. This definition of the variables introduces three problems. The first is an omission: the variables do not contain enough information to reconstruct the trajectories of the individual digits. Three additional coordinates are needed to describe the position of the grip relative to the wrist. The second problem is that the wrist is not transported to the object, but to a position about 15 cm away from it in an unknown direction (see for instance Figures 1B, 1C). The third problem is that by this definition, the rotations of the wrist are a part of the grip component. As only proximal muscles move the wrist, distal muscles alone cannot control the grip component.

We conclude from the discussion of the anatomical argument that neither the correspondence between the transport component and movements of proximal segments, nor the correspondence between the grip component and the activation of distal muscles, are unequivocal. It is therefore not justified to map the anatomical attributes "proximal" and "distal" onto the movement variables "transport" and "grip" in the control of grasping.

1.3 Modeling

The transport-grip approach has been used extensively in describing experiments on grasping, but it has not inspired many scientists to model grasping. The only model for grasping we are aware of is that of Hoff and Arbib (1993). Their model controls the transport and grip components on the basis of a minimum-jerk approach, combined with on-line feedback controllers. The transport component is generated by an element similar to the one for pointing. For the grip component, two extra controllers are used. These controllers are not based on general principles of motor control but are designed to let the model reproduce the consistent experimental findings in studies on grasping. The most consistent finding is that the maximum grip size increases with the size of the object (Jeannerod, 1981), with a slope of about 0.8. This finding was used to design a "preshape controller." A second consistent experimental finding is that the maximum opening of the grip occurs in the second half of the movement, at 60–80% of the movement time (Jeannerod, 1984). This finding was used to design a "hand closure controller." To incorporate more experimental data, an extra cost function was used which introduced a general tendency to close the hand (Hoff & Arbib, 1993).

The model of Hoff and Arbib (1993) was designed to explain the characteristics of perturbation experiments, and it reproduced the kinematics of such experiments very well. The control of the timing and of the size of the grip component was implemented on the basis of experimentally observed behavior; it was not designed to explain these characteristics. Can we predict these experimental characteristics using a model that is not based on parameters extracted from experimental results?

2 — Our Alternative Approach

2.1 Formulating an Alternative Description

Wing and colleagues have argued that it is not the wrist but the thumb that is transported during grasping (Haggard & Wing, 1997; Wing & Fraser, 1983; Wing et al., 1986). One of their arguments for assuming that the motion of the thumb is planned is the development of variability of the thumb's path during the movement (Haggard & Wing, 1997): the variability in the thumb path decreases near the object, whereas that of the wrist remains constant. As the variability of the finger develops in a similar fashion as the thumb (Haggard, personal communication; Paulignan et al., 1997), one could argue that the finger is transported too. This is the basis of our approach. We thus abandon the grip as a variable in our model of grasping.

Our alternative approach is directly based on the requirements of the grasp. For a stable grasp, fingers should be placed at positions on the surface in such a way that the line connecting the fingers is perpendicular to the surface on both sides and goes through (or above) the center of gravity of the object (see for instance Iberall et al., 1986; MacKenzie & Iberall, 1994). The accuracy with which the digits must be placed depends on the weight and friction of the object (Fikes et al., 1994): the required accuracy is highest for heavy or slippery objects. To plan how to grasp an object, the nervous system begins by determining suitable *positions* on the object's surface. How these positions are determined is a problem beyond the scope of this paper. Our approach is to leave out any other information processing (determining the object's size, etc.) and regard grasping as nothing more than moving the thumb and fingers to these positions.

At first this approach may appear implausible, because the simplest way to move the finger or thumb toward a position on the surface is along a straight line. This is indeed what is generally found in pointing (Flash & Hogan, 1985; Morasso, 1981). In prehension, however, the trajectories are not straight at all. They curve strongly near the target, where the grip begins to close (see for instance Paulignan et al., 1991a). How can the digits' movement during pointing and grasping be based on the same principles?

Pointing movements are not always straight. Even when the movements are slow, and subjects are explicitly instructed to move in a straight line, the trajectories are systematically curved (de Graaf et al., 1991). We recently reported (Brenner & Smeets, 1995) that these small curvatures of slow pointing movements depend on the orientation of the surface to which the movements are directed, such that the trajectories tend to end perpendicular to the surface. We propose that our rule —trajectories approach surfaces more or less perpendicularly—is a general rule in motor control.

We argue that the tendency to approach surfaces perpendicularly, and thus the curvature of the trajectories, is determined by the constraints of the movement. A first constraint is that given the natural inaccuracies in human visuomotor control, a perpendicular approach is the only way to ensure contact near the desired positions (see Figures 2A, 2B): when approaching along a straight line, small variability in the movement path will cause rather large errors in position on the surface. Furthermore, the object can easily be missed or pushed over due to a small error. A second constraint on the approach is that the fingers should not slip when the surface is touched. To avoid slipping, the direction of the applied force (and thus the direction of approach) should be close enough to perpendicular (see for instance Iberall et al., 1986, and also Figures 2C, 2D). If we can formulate these constraints (i.e., that the digits must approach the surface more or less perpendicularly) in terms of a pointing model, we will have a model that can, in principle, generate trajectories for grasping movements.

2.2 Developing the Model

Assuming that the control of grasping is based on the same principles as the control of pointing, we can begin using the knowledge of pointing movements to build a very simplistic model of grasping. At this point we wish to avoid any consideration of the mechanics of limbs and joints. We want to use a model that is based on a formulation of the trajectory formation in terms of kinematics of the end-effector. The minimum-jerk model, developed by Flash and Hogan (1985), is a logical choice because it is formulated as an optimization with constraints at the beginning and end of the movement. The latter constraints are the place to incorporate the perpendicular approach to the objects in the model. We do not claim that this is the best model for describing pointing (or grasping). The model is rather simple: it has no parameters that can be used for curve fitting. As a result, it cannot incorporate all experimental findings of pointing movements. For instance, it cannot account for the experimentally found asymmetries in the velocity profile (Nagasaki, 1989). Therefore, one cannot expect that it will account for all experimental findings on grasping. The advantage of this simplicity, however, is that the

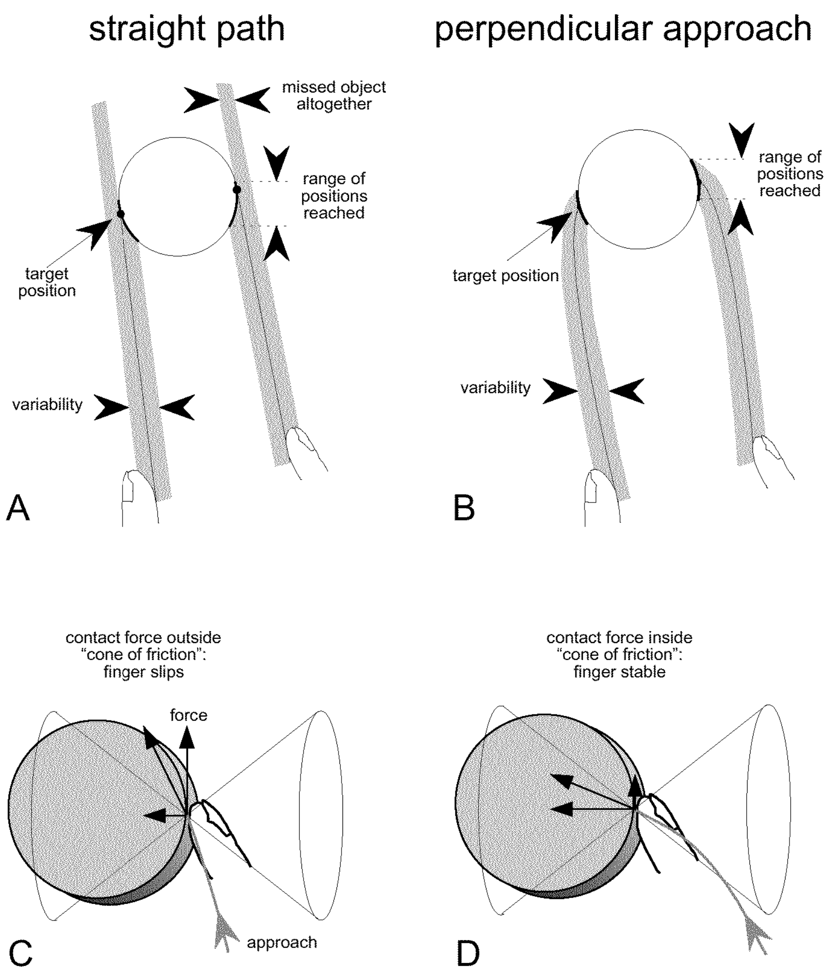

Figure 2 — Trajectories of thumb and finger toward an object. A, B: If the approach is along straight paths (A), spatial variability will cause large errors in the final grip. If the object is approached via curved paths (ending perpendicular to the surface, B), spatial variability will have a more limited effect on the accuracy of the final grip. C, D: To manipulate the object, one must exert a force on its surface. When the digits contact the object's surface, the activity of the muscles that caused the preceding movement produce force in about the same direction. For a stable contact, the component of this force parallel to the object's surface must be canceled by friction, otherwise the finger will slip. This friction is limited by a value proportional to the component of the force perpendicular to the object's surface. The "cone of friction" (the size of which depends on the index of friction of the finger-object contact area) separates stable forces from ones that will lead to slipping of the digit. If the approach is more or less parallel to the surface (C), the friction will be too low to prevent slipping of the digit. If the approach is more or less perpendicular to the surface (D), the friction will keep the digit stable.

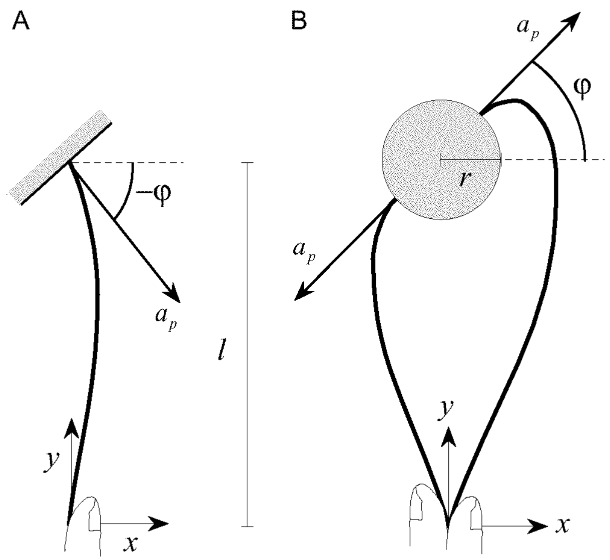

Figure 3 — The geometry used to model our approach: (A) for pointing, (B) for grasping.

results are a clear outcome of the assumptions of the model, and not the result of careful parameter adjustment.

To model pointing movements to an isolated position in space, the parameters are the movement time, the initial and final positions, and a velocity and acceleration of zero at both the beginning and end of the movement (Flash & Hogan, 1985). As argued previously, the digits' movements when grasping tend to approach the object's surface perpendicularly. We modeled this by taking a nonzero deceleration (perpendicular to the surface) at the end of the movement. The value of this final deceleration depends on the precise nature (required speed and accuracy) of the grasp. To link the notion of perpendicular approach—which is a characteristic of the path, and thus independent of time—with the model's constraint on the final deceleration, a parameter related to time, we scaled the final deceleration by the squared movement time. The result is an "approach parameter" a_p, which has the dimension of length and is oriented perpendicular to the surface (see Figure 3A). When modeling such movements, the approach parameter is a measure of the way the surface is approached: the larger this parameter, the more perpendicular the approach.

The value of the approach parameter depends on the relationship between the required accuracy of the positioning of the fingers and the variability in their movement paths. One factor determining the variability is the movement time: faster movements are more variable (as documented by Fitts & Peterson, 1964, for pointing). For grasping, a similar relationship between speed and variability has been found: Wing et al. (1986) reported that the variability of the position of the thumb near contact was 50% higher when grasping as fast as possible than when the movement was executed at normal speed.

The accuracy with which a digit is positioned on an object's surface can be increased in two ways: by a more perpendicular approach (larger approach parameter) or by executing the movement with less variability (i.e., more slowly). The way we use our model to predict the effects of experimental conditions on grasping behavior is by translating the changes in the required accuracy into changes in the value for the approach parameter: the more accurate the movement has to be, the larger the approach parameter. As argued above, the movement time may also vary with the required accuracy. The size of the predicted effect of the approach parameter will therefore depend on the concomitant change in movement time: the more the movement time increases, the less the approach parameter will have to increase.

Going from pointing to grasping is straightforward. In this paper, we let both digits begin at exactly the same position and move in the same movement time toward a disk. Finger and thumb move to positions on exactly opposite sides of the disk, which are approached with the same value for the approach parameter (see Figure 3B). This geometry is a simple approximation of that used in many experimental studies. The results we mention in this paper are based on this approximation. In Section 3.9 we address the question of what would happen if finger and thumb were treated more differently.

2.3 Description of Model Behavior

The model is derived in the Appendix. Some aspects of the model behavior are clearly visible when examining the equations. For instance, the development of the transport component is independent of the size of the object (Equation 4). Similarly, the development of the grip component is independent of the distance of the object (Equation 5). Moreover, the development of both the transport component and size of the grip are independent of the orientation φ of the final grip (Equations 4 & 5). The effects of variation in approach parameter and object size are illustrated in Figures 4 and 5.

Figure 4 shows the model trajectories of finger and thumb grasping a 4-cm disk for several values of the approach parameter and a final grip orientation of 45° relative to the transport direction. The shape of the digits' movement paths depends on the value of the approach parameter (Figure 4A). Although finger and thumb are controlled in the same way, the trajectories of the two digits clearly differ from each other. This difference is caused by the difference in surface orientation at the end points. Not only the movement paths but also the velocity profiles differ between the digits (Figure 4B). The finger reaches a higher peak velocity than the thumb, and this peak occurs earlier during the movement. These differences between finger and thumb increase with the approach parameter. The value of the approach parameter is directly visible in the velocity profile: it is the slope of the curve at the end of the movement.

Despite the fact that the trajectories of finger and thumb strongly depend on the value of the approach parameter, their average (which we refer to as the transport component) is independent of the approach parameter. The transport component has the same bell-shaped velocity profile as a minimum-jerk point-to-point movement (solid curve in Figure 4B).

The time-course of the grip does indeed depend on the approach parameter, and its global shape roughly resembles those reported in the research literature: a

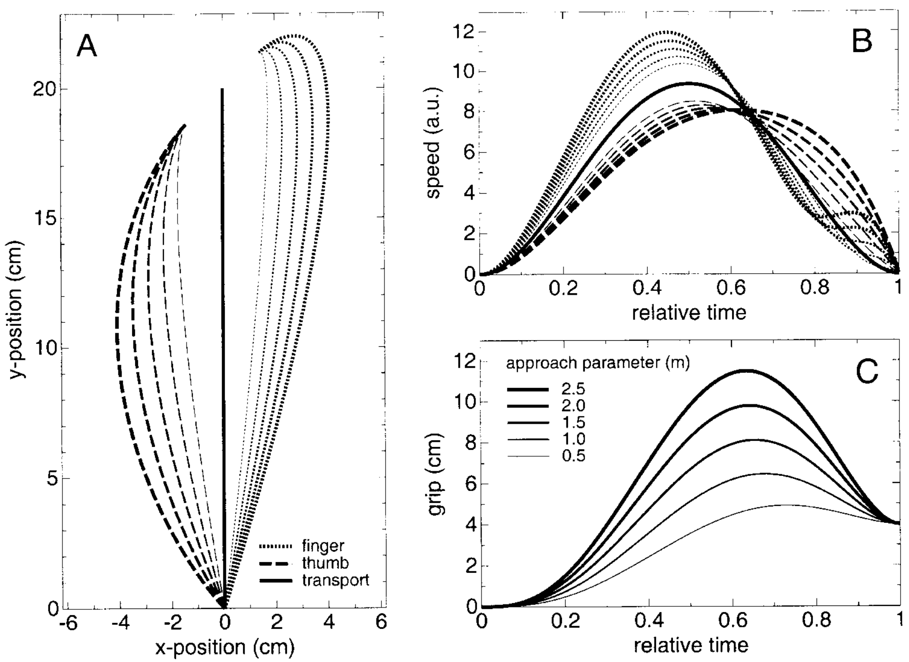

Figure 4 — A set of trajectories generated by our model for various values of the approach parameter (a_p). Disks (4 cm in diameter) at 20 cm distance are grasped with an a_p ranging from 0.5 to 2.5 m. The thicknesses of the curves are proportional to the a_p. A: Calculated paths of finger and thumb and their average (transport component). B: Velocity profiles of transport component and the movements of finger and thumb. Note that the transport component is independent of the a_p. C: Time-course of grip aperture as derived from the calculated trajectories of the digits.

maximum (larger than the object) in the second half of the movement (Figure 4C). The maximum grip aperture is larger and occurs earlier during the movement for larger values of the approach parameter.

Figure 5 shows the model trajectories of finger and thumb when grasping disks of various sizes using a constant approach parameter. It is obvious that varying the disk size leads to changes in the paths of the finger and thumb (Figure 5A). The maximum velocities of finger and thumb also vary with object size, but the timing of these maximums remains constant (Figure 5B). Again, the transport component is unaffected: it is the same for all disk sizes. The grip is affected: not only is the maximum aperture larger for larger disks but it also occurs later (Figure 5C).

Thus the main predictions of our model are as follows:

1. The transport component is independent of intrinsic object properties (e.g., size).
2. The size of the grip is independent of extrinsic object properties (e.g., distance).
3. The grip size increases and occurs *later* for larger disk sizes.

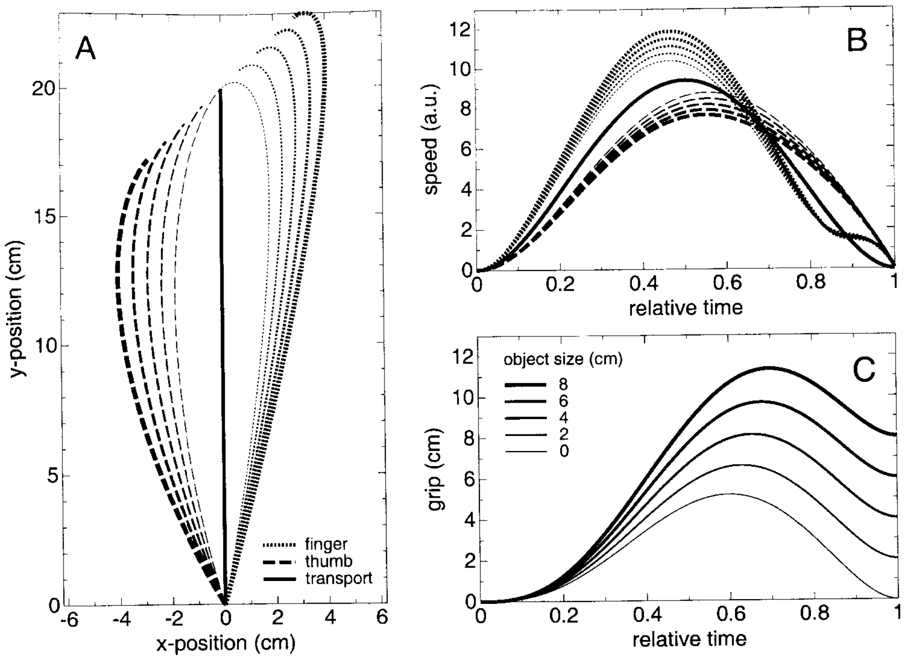

Figure 5 — A set of trajectories generated by our model for various disk sizes. Disks with diameters of 0 to 8 cm at 20 cm distance are grasped with an approach parameter of 1.5 m. The thicknesses of the curves are proportional to disk size. A: Calculated paths of finger and thumb and their average (transport component). B: Velocity profiles of transport component and the movements of finger and thumb. Note that transport component is independent of disk size. C: Time-course of grip aperture as derived from the calculated trajectories of the digits.

4. The grip size increases and occurs *earlier* if the approach parameter is increased (due to variations of other intrinsic object properties or other task constraints).

In the next section, we will discuss the quantitative predictions of the model for various experimental manipulations that have been reported.

3 — Can the New Approach Explain Existing Data?

3.1 Independence of Transport and Grip

The first two predictions of the model—that the transport component is independent of object size and that the grip component is independent of distance—are very interesting. They imply that our model generates gasping behavior that looks as if it is based on two independent visuomotor channels: one for transporting the fingers and one for shaping the grip. Our model, however, is clearly not based on independent visuomotor channels for transport and grip: it is based on the movements of individual digits. Experimental results (Jeannerod, 1981, 1984) showing the independence that our model predicts have been the basis for assuming that there are two independent visuomotor channels in the human brain. Our model shows that such apparently independent behavior could emerge from a totally different control scheme.

This finding has general implications. It shows that independent behavior of variables in motor control does not necessarily mean these variables are controlled independently. The independent behavior can emerge from the control of other variables. When building a model, one is free to choose the variables that are controlled, which allows one to make statements about the variables that are controlled in the model and how this control is achieved. When studying human behavior, one must keep in mind that various control schemes in which certain variables are controlled could be the basis of the observed behavior. Our model shows how easily one can be deceived, emphasizing that one should be very careful when claiming that certain variables are controlled in human behavior. We will therefore not claim that the trajectories of finger and thumb are controlled in human behavior; we claim only that their behavior is more easily understood than that of the classical variables.

In the previous paragraphs we stressed the experimentally observed independence of the two components. However, almost all more recent experiments show some form of dependence between the two components (e.g., Chieffi & Gentilucci, 1993; Jakobson & Goodale, 1991). None of the authors have concluded from their experiments that the general picture of the early work of Jeannerod should be revised, because the dependencies were not too severe. Nevertheless, this raises the question of how such dependencies can follow from our model.

Our model predicts that the transport and the grip component are independent. However, this prediction only holds if the constraints are the same for finger and thumb. For instance, it does not hold if the finger and thumb have different movement times or approach parameters. In the latter case, the transport component depends on the values of the approach parameters, and thus on intrinsic object properties. In Section 3.9 we will discuss the circumstances in which the approach parameters are likely to be different between finger and thumb.

3.2 Effect of Object Size on Grip Parameters

Since the pioneering work of Jeannerod (1981, 1984), the relationships between object size and grasping parameters have been studied extensively. We found 35 studies presenting values of various parameters in relation to object size. This makes it possible to identify relationships that are insensitive to variations of instructions, experimental design, and methods of data analysis. The classical description does not predict these relationships. It only describes the observation that the maximum grip aperture correlates with object size, and that it occurs during the second half of the movement, at the time of maximum deceleration of the transport component, regardless of object size (Jeannerod, 1981). Hoff and Arbib's (1993) model was designed to reproduce these relationships, but it does not predict them.

Our model can generate quantitative predictions for the effect of object size. To compare the results with experimental data, we determined two parameters from our simulations: "maximum grip aperture" and "time to maximum grip aper-

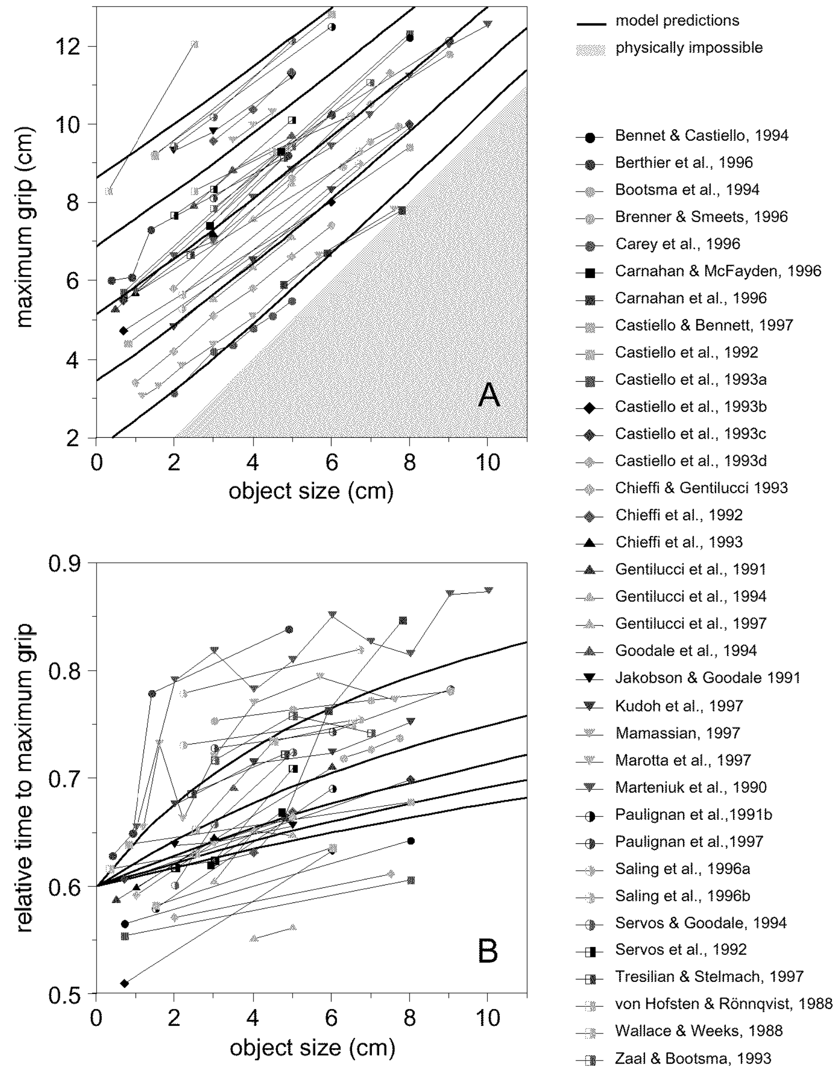

Figure 6 — Experimental values (see Table 1 in Appendix) and model predictions (Appendix) for various parameters of the reach to grasp. A: Our model predicts an almost linear increase of the maximum size of the grip with object size. The model curves are for approach parameters (a_p) ranging from 0.5 m (lower curve) to 2.5 m (upper curve). The slope of the relationships is remarkably consistent, and very close to the one predicted by our model. The intercept of the relationship varies strongly between experiments, which is consistent with it being determined by marker placement and various constraints of the task (which influence the a_p). B: Our model predicts that the time to maximum grip size (as a percentage of movement time) should increase with object size from 60% to >75%. The model curves are for a_p ranging from 0.5 m (upper curve) to 2.5 m (lower curve). The experimental data show a lot of variability but the general pattern conforms to these predictions.

ture." To simulate the variations in instructions and experimental conditions, we used five (arbitrary) values for the approach parameter. The results of the model calculations are shown as the thick curves in Figure 6. These curves are purely theoretical predictions; no parameters were fit. For each value of the approach parameter, the calculated path is independent of the movement time.

To compare the model predictions with experimental data, we plotted the experimental data we found in the literature in the same figure. We also performed linear regressions for both experimental parameters in relation to object size for the data from each study, as well as for the predictions of our model. The model predictions follow the experimentally observed trend very well.

For the maximum aperture of the grip, our model predicts an almost linear increase with object size (Equation 8 in the Appendix, Figure 6A). The predicted offset of the relationship between maximum grip size and object size depends linearly on the approach parameter, and can therefore have any positive value. As the predicted relationship between maximum grip size and object size is not exactly linear, the slope of a linear fit to this relationship depends slightly on the approach parameter and the range of object sizes included. We used five values for the approach parameter (0.5–2.5 m) to span the experimentally found range of grip sizes. Fitting disk sizes between 0 and 10 cm, we obtained an average model value of 0.81 for the slope. The average of the 35 experimental values we found in the literature was 0.82, which did not differ significantly from the prediction (t-test, $p = 0.90$). Figure 7A shows a histogram of the experimental values we found for the slope of the relationship between maximum grip size and disk size. The shaded area indicates the region in which our model predicts the slope to be.

There is a large variability in the offsets of the relationship between maximum grip size and object size. Part of the variability can be explained by different values of the approach parameter for different experiments (see Section 3.8). Another source of the variability is the way in which the grip size is determined from experimental data. The position of the markers on the digits varies between experiments, which introduces an offset (of up to 3 cm) in the measured grip size. Some researchers have corrected for this offset while others have not. As we could not predict any value for the approach parameter, we could not use the offset in any way to compare the model with experimental results.

The model also predicts the time at which maximum grip occurs. This varies from 60% for very small objects to 80% for large objects grasped with a small approach parameter. In Figure 6B we plotted the time of maximum grip from 32 experiments together with our model predictions for the same five values of the approach parameters as in Figure 6A. Two general features of all the experiments are predicted: the maximum grip occurs in the second half of the movement, and it occurs later for larger objects. The third prediction—maximum grip size at 60% of the movement for extremely small objects—does not hold for all individual experiments. To test whether this prediction holds for the average experiment, we compared the results of linear regressions on the experimental and model results, using the same five arbitrary values for the approach parameter. The predicted intercept was on average at 61% of the movement; the average for the experimental data was 60% and did not differ from the predicted value ($p = 0.76$). Figure 7B shows a histogram of the experimental values we found for the intercept of the relationship between time of maximum grip size and disk size. The shaded area indicates the region in which our model predicts this offset to be.

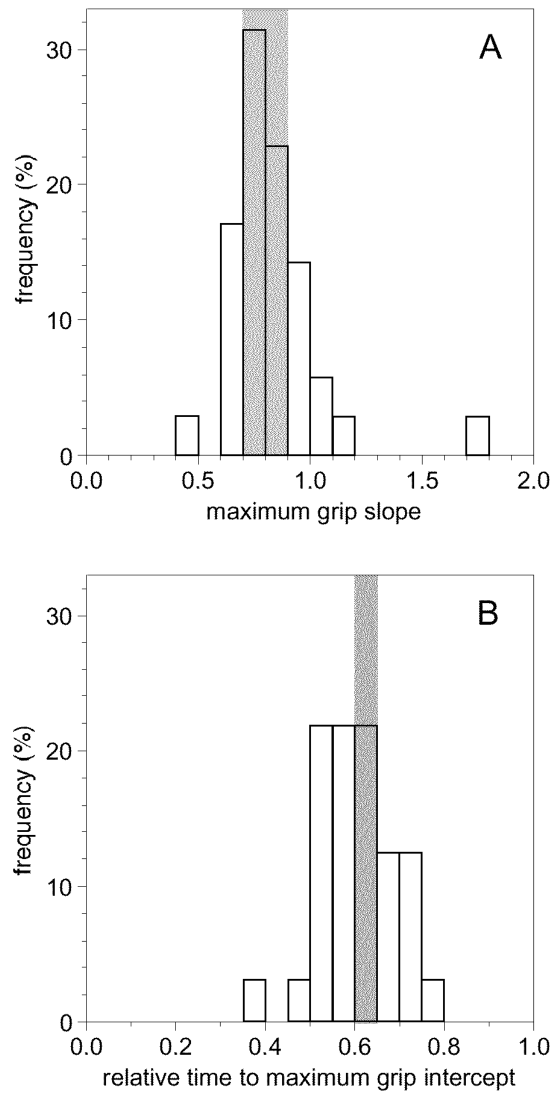

Figure 7 — Histograms comparing model calculations (grey bars) with experimental results (transparent bars) for the main predictions for parameters of the grip. A: The distribution of the slopes of linear fits to the relationship between *maximum grip size* and *object size* for the data of 31 experiments (see Figure 5A) has a sharp peak near the predicted value. The outlier on the right (a value of 1.7 reported by Wallace & Weeks, 1988) is twice the predicted value. It could be that Wallace and Weeks reported the radius of their objects instead of the diameter (they are confident of their dimensions as published but could not verify them because they no longer have the dowels used in the experiment; Wallace, personal communication). B: The values for the intercept of the linear fit to the relationship between the *time of maximum grip* and *object size*, for data of 29 experiments (Figure 5B), is also distributed around the predicted value.

For the slope of the relationship between time of maximum grip and object size, the predicted value depends on the approach parameter. As we chose the values of the approach parameter to accommodate the experimental values of grip size, comparing the model prediction with experimental values gives some information about the value of the model. The slopes did not differ: the slope was 1.8%/cm for the experiments and 1.2%/cm for the model calculations (*t*-test, $p = 0.31$).

Part of the variability in the timing measures from individual experiments could be due to variability in the exact definition of the onset and end of the movement. As an example, we will regard a model movement of 800 ms over 20 cm to a very small object. The maximum aperture will be at 480 ms. If we determine the onset of the model movement by a position threshold of 0.4 mm (rather accurate), we detect movement onset 50 ms after the movement began. Due to this delay, the peak opening will appear at 430 ms, which corresponds to 57% instead of 60% of the movement. A similar but opposite effect can be caused by the choice of criteria for defining the end of the movement. Thus, the definition of movement boundaries could be a main reason for the difference between experimental results and our predictions.

We conclude that our model for the independent transporting of the finger and thumb predicts both of the studied effects of object size on grip component. The classical description has no prediction for these effects. Note that our model results are based on the assumed absence of effects of object size on the approach parameter in the ensemble of experiments, as discussed in the next section.

3.3 Effects of Object Size on Transport Parameters

When calculating the model predictions in the previous subsection, we assumed that accuracy constraints, and thus the approach parameter, are independent of object size. As discussed in Section 2.2, accuracy constraints on the task can affect both movement time and approach parameter. Our model makes no quantitative predictions for movement time. Qualitatively, we predict that when comparing tasks with similar accuracy constraints, the movement time will be similar too. Assuming that the accuracy constraints are independent of object size, the movement time should be independent of it as well. Movement time is provided—for objects of different sizes—in 32 of the experiments in the ensemble we use. We determined for each of these experiments a linear regression between movement time and object size. The average of the slopes of these relationships did not differ significantly from zero ($p = 0.34$).

To test the above-mentioned assumption, we studied another parameter of the transport component: the time of peak velocity. A characteristic of less accurate movements, which is not captured by our model, is that the peak velocity occurs later in the movement (as shown for pointing by Bullock & Grossberg, 1988; MacKenzie et al., 1987; and for grasping by Marteniuk et al., 1990). Our model predicts that the peak of the transport velocity will occur at 50% of the movement time, independent of object size. In all, 28 of the 35 studies provide data on the timing of the peak transport velocity. We determined for each of these 28 experiments a linear regression between the time of peak velocity and object size. The average intercept was at 41% of the movement, and the slope did not differ significantly from zero ($p = 0.13$).

Thus, the model predicts that the parameters of the transport component are independent of the size of the object, which corresponds to the average experimental result. Moreover, the experimental findings indicate that the accuracy constraints in the ensemble of experiments did not depend on object size, and therefore this justifies the use of a single approach parameter for all object sizes when comparing our model predictions to the ensemble of 35 experiments in Section 3.2.

3.4 Effects of Contact Surface Size

In the previous subsections we discussed quantitatively the effects of object size (i.e., size of the grip aperture when the object is grasped) on parameters of the movement. Another dimension of the object is also important for the formation of the grip: the size of the contact surface influences the required accuracy of the approach. A smaller size of the contact surface will generally require a larger accuracy, which corresponds to a larger approach parameter (and longer movement time) in our model. Our predictions are therefore that objects with smaller contact surfaces but the same size are grasped more slowly with a larger maximum grip aperture, and that this maximum aperture occurs earlier in the movement. Following the classical description and considering the speed/accuracy trade-off, Bootsma et al. (1994) predicted for the transport component that decreasing the contact surface size would increase the movement time and lead to a relatively later peak velocity. Both predictions were experimentally confirmed (Bootsma et al., 1994; Zaal & Bootsma, 1993). Bootsma et al. predicted no effect of contact surface size on the grasp component, considering the classical independence of transport and grasp. Did the experiments show an effect of contact surface size on the grasp component?

Zaal and Bootsma (1993) compared grasping of round and flattened objects. The difference between these two types of objects was the size of the contact surface, which was at least 2 cm. They found larger maximum grip apertures which occurred earlier during the movements for the objects with the smaller contact surfaces, as we would predict. Bootsma et al. (1994) did a similar experiment with smaller sizes of the contact surface. They used rectangular objects ranging in width from 0.5 to 2.0 cm. They also found that the maximum grip occurred earlier for smaller contact surfaces, but they found smaller grip sizes for smaller contact surfaces.

The size of the actual contact surface can also be varied by the way in which the object is grasped. When grasping an object using the whole hand, the contact surface is larger than when grasping the same object using two fingers. The movement can therefore be less accurate, and the approach parameter can therefore be smaller, when using whole-hand prehension than when using a precision grip. Thus the prediction for experimental parameters is that the maximum grip aperture will be smaller and will be reached later for whole-hand prehension. The experiments by Gentilucci et al. (1991) indeed found both predicted effects.

Contrary to the classical description, our model predicts an effect of object size on both the timing and amplitude of maximum grip aperture. For the three experiments discussed, five of six experimental observations follow our predictions. The effect of contact surface size on the maximum grip aperture reported by Bootsma et al. (1994) follows neither our prediction nor that from the classical view.

3.5 Effects of Other Intrinsic Object Properties

In Section 2.1 we discussed two aspects that constrain the placement of the fingers. One is that the fingers should be positioned accurately enough so that the center of mass is below the line connecting the two fingers. If not, the object will begin to rotate. How precise this positioning should be depends partly on the weight of the object. The second aspect is that the fingers should not slip when they begin to exert force. The required accuracy to prevent slip depends partly on the surface roughness of the object. Whether these two aspects actually constrain the movement of the fingers depends on the combination of several properties—shape, weight, and surface roughness—and will vary between experiments.

Our model predicts that intrinsic object properties other than size (e.g., weight, surface roughness) can affect the required accuracy. If so, a change in that property will change the approach parameter (and thus the grip) as well as the movement time. The classical description makes no predictions for the effect of these properties on grasping. Three such intrinsic properties have been studied: weight, surface roughness, and fragility.

If the weight constrains the positioning of the fingers, we expect subjects to strive for a higher accuracy for heavier objects. This can be achieved by moving more slowly or by approaching more perpendicularly, or by a combination of both strategies. The first strategy will lead to longer movement times. The second strategy (increasing the approach parameter) will result in a larger grip earlier in the movement for heavier objects. Weir et al. (1991a) studied the effect of weight on grasp kinematics. They report that changing object weight did not change any relevant variable significantly. Steenbergen et al. (1995) compared the reach to grasp an empty cup with one to grasp a cup partially filled with cold coffee. For the filled cup, the authors report a nonsignificantly larger aperture, which occurred significantly earlier during the slower movement.

If friction (surface roughness) constrains the positioning of the fingers, slippery objects must be approached more accurately (see Section 2.2 and the discussion in Fikes et al., 1994). The approach parameter will therefore be larger for objects with slippery surfaces, leading to a larger grip earlier in the movement. Furthermore, movements toward slippery objects will be longer. Experiments on the effect of surface roughness (Weir et al., 1991b) showed no effect on maximum grip size. For the relative time of the maximum aperture, Weir et al. report a large effect in the predicted direction. A second significant effect was a longer movement time for the objects with slippery surfaces (also reported by Fikes et al., 1994).

One would not expect the required accuracy to depend on how fragile the object is. However, one does expect that the contact must be more gentle for fragile than for firm objects. In terms of our model, the approach parameter is equal but the final deceleration should be smaller. This can only be achieved by increasing the movement time. The equal approach parameters should yield equal grip apertures at the same relative time. Savelsbergh et al. (1996) investigated how information about fragility affects grasping. In their task, the size (1.5 cm) and shape (cylinder) of the objects was constant, only the appearance differed: transparent or black. The impression of the subjects was that the black object was less fragile. The results are exactly as our model predicts: no significant effect on relative timing or amplitude of the maximum grip, but a 70-ms longer movement time for the fragile object.

In a review, Weir (1994) concluded that information about weight, roughness, and fragility is not used for the reach to grasp. Our review of the literature leads to a different conclusion. Although not all predicted effects of intrinsic object properties on the grip component were found in all studies, all significant effects reported were in the direction that our model predicts, and no significant effects were reported for parameters for which our model predicts no effect. Our conclusion is that weight, roughness, and fragility affect the reach to grasp in the manner that our model predicts.

3.6 Effects of Limited Perception

A last kind of manipulation we want to discuss in relation to the approach parameter is manipulation of the perceptual information on object position. If this information is less accurate, one can expect inaccuracies in the final grasp. We predict that the approach parameter will be larger, to compensate for these inaccuracies. This will result in a larger maximum grip aperture earlier during the movement. Again, the classical description has no predictions for the effect of this manipulation on the grip parameters. Both approaches predict that limited perception will lead to longer movement times.

Berthier et al. (1996) showed that when visual information was reduced by having subjects grasp a glowing or sounding object in the dark, the maximum grip aperture increased and occurred earlier during the movement. Similarly, Sivak and MacKenzie (1990) found that when subjects were forced to use peripheral vision to grasp an object, the maximum grip aperture was larger and occurred earlier during the movement than when using central vision or full vision. Chieffi and Gentilucci (1993) found larger grip apertures, which occurred earlier in the movement for haptically rather than visually presented objects. Wing et al. (1986) compared grasping with eyes closed to normal grasping, and found that subjects used a larger aperture, which occurred earlier during the movement for the blind grasp. Except for the study of Wing et al. (1986), in which no effect was found, all studies reported an increase of movement time when visual information was reduced. Thus, both of our models' predictions for the effects of limited perception on grip parameters are found in all four studies on this subject.

3.7 Effects of Timing Constraints

In Section 3.1 we argued that our model predicts that the transport and grip should appear to be independent. However, this is only the case if the manipulations that induce changes in the transport component do not influence the approach parameter. We introduced the "approach parameter" as a way to formalize the constraints imposed by the variability in the movements (Figure 2). Higher variability requires a larger approach parameter, for which our model predicts a larger grip size earlier in the movement. As discussed in Section 2.2, another way to deal with high variability is to decrease the speed to increase the accuracy (speed/accuracy trade-off). The subject is thus more or less free to increase the accuracy of the digits' placement by either decreasing the speed or by increasing the approach parameter (or a combination of both). A consequence of this freedom is that manipulating the movement time while keeping other constraints constant should change the approach parameter. Our model predicts that increasing the speed will lead to a larger approach parameter, and thereby to larger grip apertures earlier in the movement.

Wing et al. (1986) compared grasping as fast as possible with normal grasping. When the movement was performed as fast as possible, the maximum grip size was 15% larger than when the movement was performed at normal speed. However, it occurred later during the movement. In their Experiment 3, Wallace and Weeks (1988) used a manipulation similar to that of Wing et al. (1986). Subjects were instructed to grasp a small dowel in either 200 or 400 ms. When the allowed movement time was short, the grip size was larger and occurred earlier during the movement, as predicted. This result was confirmed in a subsequent study using longer movement times (Wallace et al., 1990).

Wallace et al. (1992) and Carnahan and McFayden (1996) constrained the timing of the grasp by letting their subjects grasp moving objects at a constant position. The faster the object moved, the faster the arm had to move to grasp it at that position. In these studies, a twofold timing constraint is imposed by the target speed. The first is that the hand movement is faster and thus more variable for faster targets, as in the studies by Wing et al. (1986), Wallace and Weeks (1988), and Wallace et al. (1990). The second is that variability in timing of the arm movement results in larger variability in object position for faster targets. Therefore our predictions should definitely hold for these studies. Both studies indeed reported larger grip apertures earlier in the movement for faster objects.

Saling et al. (1998) constrained the timing of the grasp by placing an obstacle in the hand path between the starting position and the target object location. Without an obstacle, the movements were faster than with an obstacle in the movement path. The maximum grip size was larger and occurred earlier in the faster movements than in the slower movements.

All six experiments show the increase of grip size with movement speed that our model predicts. Our model also predicts that the maximum grip will occur earlier in faster movements. Five studies show this effect, but one study reports the opposite effect. Remember that in the classical description, the effects of the accuracy are restricted to the transport component (e.g., Bootsma et al., 1994), so no effect on grip is predicted.

3.8 *Variability in Experimental Results*

Our model is very simple. According to the model, variability in the measured grip parameters can only have two sources. Either the perceived positions at which one intends to place the digits on the object vary, or the approach parameter does. The former will occur when grasping is performed in conditions of limited visual information. The latter will occur when object properties are not consistently estimated, for instance due to experience during earlier trials. For variability in the movements caused by variations in the approach parameter, our model predicts related effects between the timing of the maximum grip aperture and its size: if the grip is larger, it will occur earlier (for the same object).

The relationship between the timing of maximum grip aperture and its size of course also depends on the size of the object. To be able to average across object sizes, we use the variable "extra grip": the difference between maximum grip aperture and object size. The predicted relationship between the timing of the maximum of the extra grip and its size is almost independent of the size of the object. This relationship is plotted as continuous curves in Figure 8 for three disk sizes. Low values of the approach parameter result in little extra grip late in the movement (upper left). High values of the approach parameter result in large extra grip much earlier in the movement. Again, no parameters were adjusted: the curves are the direct predictions of the model.

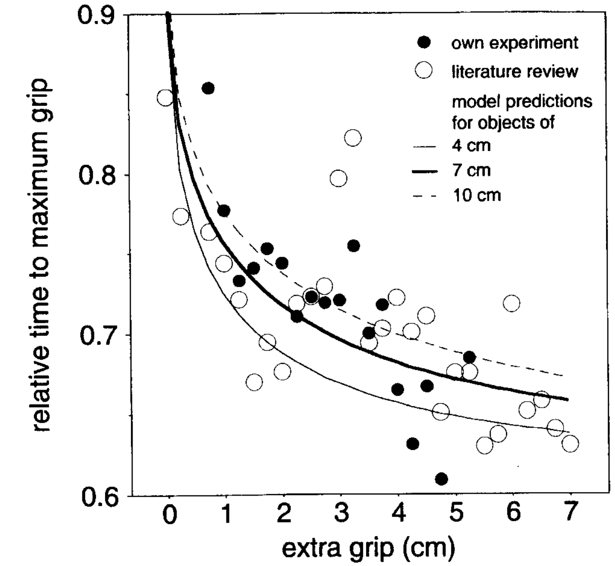

Figure 8 — Contribution of variability in the approach parameter to variability in grasp parameters. The former will cause simultaneous variations in the timing and size of maximum aperture. Curves show the predicted relationship—when a_p varies—between the timing of the maximum aperture and the "extra grip" (difference between maximum grip aperture and object size) for objects of 4-, 7-, and 10-cm diameter. The symbols are experimental values, averaged in bins of 0.25-cm extra grip. Filled symbols show the variations within one experiment (Brenner & Smeets, 1996), open symbols show variability between various experiments (see Appendix).

To examine whether variations in the approach parameter could account for experimentally observed variability, we reanalyzed the experimental data of Brenner and Smeets (1996). All data points are averaged over subjects and object sizes into 0.25-cm wide bins of extra grip. The data in Figure 8 (filled symbols) follow the predicted relationship fairly well: for trials with little extra grip, the maximum aperture occurs near the end of the movement, whereas for trials in which the hand opens much wider than the object, the maximum aperture is at about two-thirds of the movement time. Thus, within this experiment, variability in approach parameter can explain part of the correlation between the observed variability in grip parameters.

The variability in the average experimental values plotted in Figures 6A and 6B is indeed not completely due to noise: the variations between experiments in maximum aperture are related to the variations in timing of the maximum aperture. To compare this correlation with our model prediction, we averaged all data points across studies and object sizes into 0.25-cm wide bins of extra grip. The resulting data are plotted in Figure 8 (open symbols). Each symbol is thus the average of all conditions which resulted in a certain amount of extra grip. For experiments in which the objects were grasped with maximum apertures that were barely larger than the object, the maximum grip occurred earlier than in experiments in which the grip was larger. When comparing different experiments, additional sources of variability are introduced, for instance the placement of the markers and the definition of the onset and end of movement. Despite these other sources of variability, the variability in the approach parameter describes the data fairly well.

3.9 Extending the Model: Interactions Between Transport and Grip

In describing the model results, we showed that our model predicts—as the classical view assumes—that the transport and the grip component are independent. In experiments this is not always the case.

In the previous subsections we discussed the predictions of a very simple model. The model has only one parameter but can nevertheless explain several experimental findings. To make the model that simple, we made various assumptions. For instance, we assumed that the accuracy constraints were the same for both digits and that there were no constraints during the movement. This simple model predicts, as the classical view assumes, that the transport and the grip component are independent. In experiments this is not always the case. Our model can only explain such experimental findings if we allow it to become more complex.

Recently, very clear examples of a dependence of the transport component on the grip component were presented (Timman et al., 1996a, 1996b). Timman et al (1996a) introduced an additional grip task during the movement: subjects had to close and reopen their grip while reaching for the object. They found a large effect of this manipulation of the grip on the transport component: not only did the movement time increase by 200 ms but the velocity profile of the transport component changed as well: it showed a minimum at the moment of closure. Timman et al. (1996b) studied the effect of initial grip size on the grasping movement. If subjects started with a maximal grip opening, they began their movement by closing the grip to a local minimum, subsequently reopening it to a second maximum, and then closing it to grasp the object. An interesting observation was that when the grip started to reopen, the transport component decelerated. Thus the variation in grip size can change the velocity profile of the transport component of the movement.

Already in his first paper, Jeannerod (1981) hypothesized a hierarchical relationship between the two independent channels. He explicitly predicted "an alteration of the dynamics of grip to fit with those of transportation." However, a dependency of the transport-component on characteristics of the grip, as found by Timman et al. (1996a, 1996b), cannot be explained using the classical approach.

Our model is also unable to describe the experiments of Timman et al., as it is based on constraints at the end of the movement only. When introducing constraints during the movement (as in Timman et al., 1996a) or at movement onset (as in Timman et al., 1996b), one has to incorporate these constraints in the model. We do not know what would result from such an extension of the model. Increasing the curvature of the movement path results in a reduced velocity in pointing (Abend et al., 1982; Pollick & Ishimura, 1996), in drawing (Lacquaniti et al., 1983; Viviani & Terzuolo, 1982), and in grasping, as we will show in Section 4.3. This relationship follows directly from attempting to minimize jerk (Flash & Hogan, 1985). In the experiments of Timman et al. (1996a, 1996b), the curvature of the digits' paths is high near the additional closure introduced by their manipulations.

We therefore expect that extending our model with constraints leading to an additional closure will yield a low velocity of the digits (and thus of the transport) near that position, which is what Timman et al. (1996a, 1996b) report.

In our model, the parameters of transport and grip are independent of the direction of movement and the final orientation of the grip. This is not what has been found experimentally (Gentilucci et al., 1996b; Paulignan et al., 1997). The reason for the independence in our model is that finger and thumb start at the same position, without constraining each other's motion. In real life, starting with finger and thumb in contact will constrain their movements: the initial direction of a digit's movement cannot be in the direction of the other digit. Furthermore, during the movements, the digits should collide neither with each other nor with the object. When the difference between the initial and final orientation of the grip is not very large and is more or less perpendicular to the direction of motion, these constraints do not interfere with the trajectories our model predicts. In other situations, these constraints must be incorporated in the model.

Finally, we simplified the model description by assuming that the approach parameter is the same for the finger and thumb. When regarding the accuracy constraints for both digits, clear differences can be observed. For instance, the position at which the thumb contacts the object is (in most situations) in view, whereas the finger contacts the object at a position on the surface that is hidden by the object itself. This would justify (Section 3.6) a larger approach parameter for the finger than for the thumb. Furthermore, the thumb is larger than the finger, which could also lead to a larger approach parameter (Section 3.4). Introducing differences in the approach parameter results in more complex movements. The hand is no longer transported along a straight line, and the transport component begins to depend on the size of the object.

4 — What is the Value of the Model?

4.1 Comparing Control Schemes

In the previous sections we showed that our alternative description of grasping, modeled by a minimum-jerk approach, could explain many features of grasping which were unexplained by the classical description. We further showed that the formulation of grasping in terms of transport and grip has no clear theoretical advantages. What does this mean for our understanding of the control of grasping? Can we understand grasping better if we regard it as the independent movements of finger and thumb? Or should we transform the results of our calculations back to the grip and transport components, because those are in fact independent?

How can we decide which set is the most suitable to describe grasping? First we must define criteria with which to judge the control schemes. We will follow Jeannerod's (1981) concept of visuomotor channels. These channels link separate motor components to corresponding dissociable perceptual features. In general, a movement consists of the parallel activation of several channels. This concept, which Jeannerod (1981) introduced for grasping movements, has also been very successful in describing hand movements toward moving objects. The path of such a movement is controlled by visual information on target position (Brenner & Smeets, 1997; Pélisson et al., 1986; Smeets & Brenner, 1995), whereas the speed of the movement is directly coupled to the perceived speed of the object (Bairstow, 1987; Smeets & Brenner, 1995; van Donkelaar et al., 1992). These relationships hold even when the perceived information is incorrect (Brenner & Smeets, 1997; Smeets & Brenner, 1995) or changes without the subject noticing (Pélisson et al., 1986).

Our first criterion is therefore that each variable is a part of a distinct visuomotor channel: each motor variable should be linked to a distinct perceptual feature. We adopt our second criterion from a recent review of data on grasping (Paulignan & Jeannerod, 1996): the variables should be independent. This independence should not only hold for the way movements are planned but also for adjustments during the movement. Of course the channels will only be partially independent, as the task and anatomy impose many constraints. For instance, it is anatomically impossible to move the finger over a large distance without moving the thumb.

In the next section, we will discuss some experimental results in light of these two criteria.

4.2 Visuomotor Channels

We first look for evidence in favor or against the existence of the specific visuomotor channels for the various descriptions (our first criterion).

For grip size, we know of three studies that question the use of the perceived size to control the size of the grip. Aglioti et al. (1995) showed that a visual illusion that changes the apparent size of an object has no effect on the maximal aperture of the grip when reaching for it. Their interpretation of this finding was that the motor system uses other information than the perceptual system. In a recent experiment (Brenner & Smeets, 1996) we used a different visual illusion to replicate the finding of Aglioti et al. (1995). However, we showed that the illusion did indeed affect motor control: the apparently larger object was picked up using more force. Daprati and Gentilucci (1997) used the Müller-Lyer illusion to compare the effects of a visual illusion on perception with that on two motor tasks: grasping and drawing. The effect on the maximum grip during grasping (1.5%) was not only much smaller than the effect on size perception (6.3%), but also smaller than the effect on drawing (7.3%). These experiments show that although motor control is directly related to illusory perceived variables, the grip size is not directly related to the perceived size.

Our explanation for any (small) effect of size illusions on the maximum grip aperture (i.e., Daprati & Gentilucci, 1997) is that they are caused by effects on the perceived position. An estimate of this effect is given by a study of the effects of the Müller-Lyer illusion on pointing (Gentilucci et al., 1996a). Although the stimuli and experimental conditions were not exactly the same, it is remarkable that the effect on the end-point of pointing movements (1.9% in the full-vision condition) is very close to the effect on the maximum grip (1.5%).

This conclusion is supported by a totally different experiment. Chieffi and Gentilucci (1993) compared the perceived size and the grasping of visually and haptically presented objects. For haptic presentations, the subjects were blindfolded and held the object in their left hand. The subjects' task was to use their right hand either to indicate the perceived size or to grasp the object. The relationship between perceived size and object size showed a larger slope (1.2) for haptic presentation than for visual presentation (slope 1.0). The maximum grip size during grasping showed the opposite effect: the slope was smaller (0.6) for the haptic presentation than for the visual presentation (0.8). It therefore seems unlikely that the grip component of movement is controlled using the perceived size. So it is not very likely that the grip component is part of a separate visuomotor channel.

For grip orientation, Dijkerman and Milner (1998) reported a dissociation between the perceived orientation in depth of an object and the orientation of the grip. The grip orientation was linearly related to the object's orientation, whereas the perceived orientation depended in a more complex way on the object's orientation. This dissociation is not compatible with a visuomotor channel for orientation (as proposed by Stelmach et al., 1994), nor with any other visuomotor channel that relies on information about the object's orientation. It is compatible with our view that the orientation of the grip is not related to a perceived orientation of the object, but to the perceived positions at which the object can be grasped. But the critical experiment to support our view remains to be done.

The experimental evidence above does not support the idea that the grip is a part of a visuomotor channel. Our alternative description is fully compatible with the concept of visuomotor channels. Moreover, it can explain that the effect of illusions on the maximum grip aperture is comparable with the effect on perceived position, and much smaller than the effect on perceived size. In the next subsection, we will discuss whether the two channels for the movements of the individual digits are independent of each other.

4.3 Do Finger and Thumb Move Independently During Grasping?

The main assumption behind our model is that the trajectories of the digits during grasping are determined independently, and that for each digit the same rules hold as for the trajectory of a finger during pointing. We captured the characteristics of pointing by the minimum-jerk model. As discussed in Section 2.2, this is a very crude description of pointing. Is there other experimental evidence showing that the digits are controlled in the same way when grasping as when pointing? Is there other experimental evidence showing that the digits move independently?

A general aspect of biological movement trajectories is that the speed and curvature are tightly correlated. The relationship between the speed v and radius of curvature R has been studied extensively for continuous movements such as writing and drawing; Lacquaniti et al. (1983) showed that for such tasks this relationship has the form $v = kR^a$, with $a \approx 0.3$. Recently, Pollick and Ishimura (1996) showed that the same relationship holds for pointing movements but that the exponent a has a much higher value: 0.57 ± 0.05 (mean $\pm$ standard deviation) for the largest distance they used (24 cm). Re-analyzing the trajectories of finger and thumb from our own experiments on grasping (Brenner & Smeets, 1996; distance 30 cm), we found similar values: $a = 0.58 \pm 0.03$ for the thumb and $a = 0.56 \pm 0.03$ for the finger. Thus, the relationship between speed and curvature is the same for the trajectory of each digit during grasping as for the finger during pointing.

We have argued in Section 3.9 that constraints at the beginning of the movement could affect the movements of finger and thumb. Kritikos et al. (1998) studied the effect of initial hand posture on prehension. They found large effects both on the transport and grip components. These effects could be due to a specific coordination between the two components, or to constraints on the movements of each digit. To determine the source of the effects, they compared the results with an experiment using the same initial postures, but now the task was to point. The effects on the transport kinematics were similar in both tasks, from which the authors concluded that the effect of the initial hand posture on the movement kinematics was not due to a change in coordination between transport and grasp but rather to the control of movements of the individual digits.

Another argument for the independent control of the movement of finger and thumb can be found in what happens directly after the movement: the control of force. For many objects, the constraints for finger and thumb are equal, so it is not surprising that the exerted forces are also the same. Edin et al. (1992) examined whether the force is controlled for the grip as a whole or independently for each digit by using different frictional conditions at the contact surfaces. If the grip force is controlled as a single entity, the forces should be divided equally over the digits, so that the total grip force is suited to the surface with the lowest friction. But this is not what was found. The force of each digit was controlled to suit the frictional constraints at that digit's contact surface. This independent control of the digits is supported by the finding of Johansson and Cole (1994) that the coordination between digits is the same for grasping with the right thumb and index finger as for grasping with the left and right index fingers.

4.4 General Discussion

The experimental finding that object size affects the grip component, but not the transport component, has been used to argue that the transport and grip are the controlled variables. Our model shows that this is not a valid argument. In our model the trajectories of the individual digits are controlled. We only introduce the grip as the difference between the two digits in order to compare our model predictions with experimental values. Nonetheless, the resulting behavior is the same as what is found experimentally: an apparent independence between transport and grip. It is not only this "independence" that emerges from our model description. The actual relationship between various object properties and parameters of the grip also follow from the control of individual digits.

The most impressive result of our model is that the empirical relationship between the size of the target and of the grip (a slope of about 0.8) follows directly from the model, without any adjustment of parameters. Similarly, our model predicts the (relative) timing of the grip component as a function of target size reasonably well. No other model or description of grasping predicts these relationships.

A second important aspect when judging the value of our model is its generality. The model does not make any special assumptions for grasping. Neither extra controlled variables nor special coordination rules are introduced. Our approach consists of two assumptions. The first, discussed in the previous section, is that grasping is the same as pointing. The second assumption is that the accuracy constraints of a pointing task toward a surface can be described by a tendency to approach that surface perpendicularly. On this basis, we extended an existing model for pointing and applied it to each digit to describe a grasping movement. Our modified model for pointing makes explicit predictions for pointing, which should be tested to be sure that our approach is as general as we suggest.

Of course, this model is just a first attempt to use our alternative description to model grasping. We chose the minimum-jerk model because it describes pointing fairly well and because constraints on the movement (such as a perpendicular approach to the surface) can easily be incorporated. We chose the final deceleration as a way to obtain a more or less perpendicular approach to the surface. Another possibility is to implement a non-zero final velocity.

The perpendicular approach to the object's surface is not the only constraint present in most experiments. Additional constraints may be partly responsible for the variability found in the experimental data. In many experiments, for instance, subjects start with their thumb and finger in contact with each other or with an object. This imposes a constraint, which has been shown to affect the trajectories (Timman et al., 1996b). Another constraint that can affect the trajectories is the anatomical connection between the digits. In the present simulations, we have regarded the movements of finger and thumb as completely independent. This of course is not true. The anatomical link must influence the trajectories when the grip aperture approaches its anatomical limit.

If the anatomical constraint plays an important role when grasping, changing the effectors that are used to form the grip should introduce large changes in the characteristics of grasping. One way to induce such a change is to ask subjects to grasp objects using the two index fingers. In this way the grip aperture between the fingers will always be far from the anatomical limit. Tresilian and Stelmach (1997) did such an experiment, comparing unimanual and bimanual grasping of objects of different sizes. They found that both the transport and the grip components of both types of grasping "developed in very similar fashion over time in all subjects."

In this paper we have argued that it is reasonable to change the perspective on grasping from one based on transport and grasp to one based on movements of the individual digits. This change makes it possible to use existing knowledge on pointing to model grasping. We present a very simple model, which can (without any fitting or parameter tuning) explain a great deal of the coordination between transport and grasp and its variation across experimental conditions.

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Appendix

We used data from various sources to produce the graphs in Figures 6 and 7 in Section 3.2. As most papers were not intended to answer our questions, we sometimes asked the authors for additional data, reconstructed some parameters, or chose one of the various conditions tested in a paper. For each reference, Table 1 shows some details on how we obtained the data used for the four parameters discussed in Sections 3.2 and 3.3.

Table 1 Overview of Experimental Data Used for Comparison With Our Model's Predictions for the Effects of Object Size

Source	# Sizes	Maximum grip	Movement time	Time to max grip	Time to max velocity
Bennett & Castiello, 1994	6	Table 1, younger ss.	Table 1, younger ss.	Table 1, younger ss.	Table 1, younger ss.
Berthier et al., 1996	4	Table 3	Table 3	Table 3	Table 3
Bootsma et al., 1994	4	Figure 5, object width 5 mm	Personal communication	Personal communication	–
Brenner & Smeets, 1996	3	Figure 3	Re-analyzed	Re-analyzed	Re-analyzed
Carey et al., 1996	6	Figure 4, controls	–	–	–
Carnahan & McFayden, 1996	2	Experiment 2, static targets	Personal communication	Personal communication	Personal communication
Carnahan et al., 1996	3	Figure 3, controls*	Figure 1, controls	Personal communication	Personal communication
Castiello et al., 1992	2	Table 1, blocked	Table 1, blocked	Table 1, blocked	Table 1, blocked
Castiello et al., 1993a	2	Table 1, condition 2	Table 1, condition 2	Table 1, condition 2	Table 1, condition 2
Castiello et al., 1993b	2	Table 1, full vision	Table 1, full vision	Table 1, full vision	Table 1, full vision
Castiello et al., 1993c	2	Table 2, control	Table 2, control	Table 2, control	Table 2, control
Castiello et al., 1993d	2	Table 1, right, unilateral	Table 1, right, unilateral	Table 1, right, unilateral	Table 1, right, unilateral
Castiello & Bennett, 1997	2	Table 4	Table 4	Table 4	Table 4
Chieffi et al., 1992	3	Table 3, V1	Table 3, V1	Table 3, V1 (% of transport)	Table 3, V1
Chieffi et al., 1993	2	Table 5, control	Table 5, control, transport	Table 5, control (% of transport)	Table 4, control
Chieffi & Gentilucci, 1993	6	Figure 1, visual, condition D1	Table 2, visual, condition D1	Table 2, visual, condition D1	Table 2, visual, condition D1
Gentilucci et al., 1991	2	Table 3, 20 cm; assumed markers 1 cm from fingerpad	Table 1	Table 3 (% of transport)	Table 1
Gentilucci et al., 1994	3	Table 1, vision, far	Table 3, vision, far	Table 1, vision, far	Table 3, vision, far
Gentilucci et al., 1997	2	Table 1, far, control	Table 2, far, control	Table 1, far, control	–
Goodale et al., 1994	2	Table 2	–	–	–
Jakobson & Goodale, 1991	3	Table 1	Table 1	Table 1	Table 2
Kudoh et al., 1997	4	Table 1, 20 cm	Table 1, 20 cm	Table 1, 20 cm	Table 1, 20 cm
Marotta et al., 1997	3	Figure 1b, binocular	–	–	–
Mamassian, 1997	7	Figure 14, rich	Personal communication	Figure 15 / personal communication	Personal communication
Marteniuk et al., 1990	10	Figure 2	Table 1	Table 1	Table 1
Paulignan et al., 1991b	2	Table 1	Table 1	Table 1	Table 1
Paulignan et al., 1997	3	Figure 3, object at −10°	Personal communication	Personal communication	Personal communication
Saling et al., 1996a	2	Table 1, normal	Table 1, normal	Table 1, normal	Table 1, normal
Saling et al., 1996b	2	Text p. 158	Table 1, wrist	Table 1, wrist	Table 1, wrist
Servos & Goodale, 1994	3	Figure 3a, binocular	Personal communication	Personal communication	Personal communication
Servos et al., 1992	3	Figure 3, binocular	Personal communication	Personal communication	Personal communication
Tresilian & Stelmach, 1997	2	Fig. 5, unimanual, near	Fig. 7, unimanual, near	Fig. 6, unimanual, near	–
von Hofsten & Rönnqvist, 1988	3	Figure 2	Text p. 613, 50 ms after touch	Text p. 613, mean	–
Wallace & Weeks, 1988	2	Table 2, small tolerance	Table 2, small tolerance	Table 2, small tolerance	Table 2, small tolerance
Zaal & Bootsma, 1993	3	Table 1, round	Table 1, round	Table 1, round	Table 1, round

*Due to placement of markers away from fingertips, the maximum grip for the largest object was 1 cm smaller than the object size, which is physically impossible. We therefore added 1 cm to all three values for the maximum grip in this study.

Appendix (*continued*)

The general formula of a minimum-jerk trajectory is given by the polynomial equation:

$$x(t) = c_0 + c_1 t + c_2 t^2 + c_3 t^3 + c_4 t^4 + c_5 t^5 \quad (1)$$

which holds for each coordinate of the movement (Flash & Hogan, 1985).

The values for the six constants c_i can be found by applying six boundary conditions. The important new one we introduce is a non-zero acceleration at contact. To be able to easily describe the spatial properties of the trajectories (the path), independent of the timing, we use a length (a_p, the "approach parameter") to formulate this constraint. For a movement over a distance l, and a movement time MT, the constraints are:

$$x(0) = 0;\; x(MT) = l;\; v(0) = 0;\; v(MT) = 0;\; a(0) = 0;\; a(MT) = a_p/MT^2$$

Which results in:

$$c_0 = 0;\; c_1 = 0;\; c_2 = 0;\; c_3 = \frac{20l + a_p}{2MT^3};\; c_4 = \frac{-15l - a_p}{MT^4};\; c_5 = \frac{12l + a_p}{2MT^5}$$

For convenience, we introduce a normalized time t_r:

$$t_r = t/MT$$

Substitution of these parameters in Equation 1 yields:

$$x(t_r) = \left(\tfrac{1}{2} a_p (t_r - 1)^2 + l(6t_r^2 - 15t_r + 10)\right)t_r^3 \quad (2)$$

This is the equation for a pointing movement with a non-zero deceleration at contact. If the movement is in more than one dimension (i.e., if the trajectories are curved), this formula holds for each dimension, independent of the way one chooses the coordinate frame. In our example (see Figure 3), we model grasping by two-dimensional movements of finger and thumb. Both finger and thumb start their movement at the origin of the coordinate frame. The center of the object to be grasped is at a distance l along the y-axis. For convenience, we use a circular object (radius r), which is approached with equal approach parameters for both digits. The final orientation of the grip has an angle φ with the x-axis.

$$\begin{aligned}
x_{finger}(t_r) &= \cos\varphi\left(\tfrac{1}{2} a_p (t_r - 1)^2 + r(6t_r^2 - 15t_r + 10)\right)t_r^3 \\
y_{finger}(t_r) &= \left(\tfrac{1}{2} a_p \sin\varphi\, (t_r - 1)^2 + (l + r\sin\varphi)(6t_r^2 - 15t_r + 10)\right)t_r^3 \\
x_{thumb}(t_r) &= -\cos\varphi\left(\tfrac{1}{2} a_p (t_r - 1)^2 + r(6t_r^2 - 15t_r + 10)\right)t_r^3 \\
y_{thumb}(t_r) &= \left(-\tfrac{1}{2} a_p \sin\varphi\, (t_r - 1)^2 + (l - r\sin\varphi)(6t_r^2 - 15t_r + 10)\right)t_r^3
\end{aligned} \quad (3)$$

We define the transport component as the average of both digits:

$$x_{transport}(t_r) = 0$$

$$y_{transport}(t_r) = l(6t_r^2 - 15t_r + 10)t_r^3 \quad (4)$$

which is independent of both the size of the object and of the approach parameter. The trajectory is the same as an unconstrained point-to-point movement to the center of the object. The components and the size of the grip are:

$$\begin{aligned}
x_{grip}(t_r) &= \cos\varphi\left(a_p (t_r - 1)^2 + 2r(6t_r^2 - 15t_r + 10)\right)t_r^3 \\
y_{grip}(t_r) &= \sin\varphi\left(a_p (t_r - 1)^2 + 2r(6t_r^2 - 15t_r + 10)\right)t_r^3 \\
|grip(t_r)| &= \left(a_p (t_r - 1)^2 + 2r(6t_r^2 - 15t_r + 10)\right)t_r^3
\end{aligned} \quad (5)$$

The grip is thus independent of the distance l of the object. It has its maximum aperture at relative time:

$$t_r = \frac{3(a_p + 20r)}{5(a_p + 12r)} \quad (6)$$

and size of the aperture is then:

$$grip_{\max} = \frac{54(20r + a_p)^4 (15r + 2a_p)}{3125(12r + a_p)^4} \quad (7)$$

A Taylor series approximation for small values of the object diameter $d = 2r$ gives for the maximum grip aperture:

$$grip_{max} \approx 0.035a_p + (0.683 + 2.074\, d/a_p)d \quad (8)$$

From this, it can be seen that the slope of a linear regression of the relationship between maximum grip size and object diameter depends on the size of a_p relative to the disk size. The first term of Equation 8 is the offset of the relation between grip aperture and object size. To obtain realistic values of this parameter (a few centimeters), the approach parameter should be $a_p \approx 1$m. For disks with a diameter of 1–10 cm the predicted slope is between 0.7 and 0.9.

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